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Structure and variability of the marine-bird community in the northeastern Chukchi Sea ☆☆

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ABSTRACT

We examined the seasonal and interannual variation in the marine-bird community and its relationship to physical oceanography in the northeastern Chukchi Sea in 2008–2010 as part of a multi-year, interdisciplinary study. We sampled 3 study areas, each ~3000 km^2, located in the offshore northeastern Chukchi Sea: Klondike, Burger, and Statoil. We quantified the marine habitat by measuring strength of stratification, depth of the mixed layer, and temperature and salinity in the upper mixed layer. The total density of seabirds was the highest in 2009, when warm (5–6 °C), moderately saline (31–31.5) Bering Sea Water (BSW) extended across Burger and Klondike at all depths. Bird density was generally higher in Klondike than in Burger in 2008 and 2009; densities did not differ significantly among study areas in 2010, when BSW covered all 3 study areas. The relative abundance of alcids in all study areas combined increased from 2008 to 2010. Klondike was numerically dominated by alcids and tubenoses in all years, whereas Burger was numerically dominated by larids and tubenoses in 2008 and by alcids in 2009 and 2010; Statoil also was numerically dominated by alcids in 2010. Least auklets, crested auklets, and northern fulmars were positively associated with strong stratification and high salinity (>31) in the upper mixed layer, characteristics that indicated the presence of BSW. Phalaropes were positively associated with salinity but negatively associated with stratification, suggesting that well-mixed water provides better foraging opportunities for these surface-feeding planktivores. The distribution and abundance of marine birds, particularly the planktivorous species, is influenced by advective processes that transport oceanic species of zooplankton from the Bering Sea to the Chukchi Sea. This transport apparently differed among years and resulted in a broader northeastward intrusion of Bering Sea Water and greater total abundance of planktivorous seabirds in the region in 2009 than in 2008 or 2010.

1. Introduction

The seasonally ice-covered Chukchi Sea shelf is among the largest continental shelves in the world. It also is highly productive, although much of the primary production and zooplankton biomass can be attributed to the northward flow of nutrient-rich oceanic water that originates far to the south, in the basin of the Bering Sea (Springer and McRoy, 1993; Grebmeier et al., 2006). This influx of nutrients and oceanic plankton sustains a marine-bird community that would otherwise have little prey available (Springer et al., 1989). Despite an understanding of the importance of advection to the food web of the Chukchi Sea, questions remain about the spatial and temporal scales of processes that link the Bering and Chukchi ecosystems (Springer et al., 1996). Seasonal and interannual changes in advection may have profound effects on the distribution and abundance of non-breeding, staging, and migratory birds that rely on marine resources during the open-water season (June to mid-October). These relationships between community structure and oceanography must be explored if marine birds are to serve as informative indicators of ecosystem change (Piatt et al., 2007).

Descriptions of the avifaunal communities of the northeastern Chukchi Sea are rare and tend to focus on a few species of interest (e.g., Divoky, 1976), rather than considering all of the bird species that feed in the marine environment during the open-water season (e.g., waterfowl, loons, phalaropes, larids [gulls and terns], procellariids, and alcids). Attention to the marine-bird community elsewhere in the Chukchi Sea has been focused primarily on the breeding colonies at Cape Lisburne and Cape Thompson (Springer et al., 1984,1989) and on summarizing data collected

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at sea south of 69° 30′ N (Divoky and Springer, 1988; Piatt and Springer, 2003). Recent efforts to describe the circumpolar species diversity and distribution of marine birds do not include regionally important taxa such as auklets and phalaropes (Bluhm et al., 2011; Huettmann et al., 2011) that are critical to understanding energy flow in this ecosystem (Piatt and Springer, 2003).

Marine-birds can display habitat preferences for water masses and water-column structure that enhance the abundance and the accessibility of prey (Haney, 1991; Elphick and Hunt, 1993; Piatt and Springer, 2003). For example, in the northern Bering Sea and Bering Strait, bird species that rely primarily on zooplankton such as euphausiids and copepods (hereafter referred to as planktivorous species) include least (*Aethia pusilla*), and crested auklets (*A. cristatella*) and typically are associated with oceanic Anadyr Water (Springer et al., 1987; Elphick and Hunt, 1993; Piatt and Springer, 2003). In contrast, species that primarily rely on fish such as black-legged kittiwakes (*Rissa tridactyla*) and thick-billed murres (*Uria lomvia*) typically are associated with Bering Shelf Water and Alaskan Coastal Water (Springer et al., 1987; Elphick and Hunt, 1993; Piatt and Springer, 2003). Bird species that are more flexible in their foraging requirements, however, may also be more flexible in their habitat relationships. Short-tailed shearwaters (*Puffinus tenuirostris*) can consume euphausiids, shrimp, and fish (Hunt et al., 2002) and are found in all water masses of the northern Bering and southern Chukchi seas (Piatt and Springer, 2003). Within water masses, species often are segregated spatially to exploit those hydrographic features that best meet their specific foraging ecology (Haney, 1991; Russell et al., 1999; Piatt and Springer, 2003). Hence, understanding the mechanisms that link the seabird community to the marine habitat in the northeastern Chukchi Sea requires quantifying both water-mass characteristics (e.g., temperature, salinity) and water-column structure.

Historical studies conducted in the late 1970s and the early 1980s provided a snapshot of the community composition and density of seabirds in the northeastern Chukchi Sea (Divoky, 1987) but did not address the variability of this community or link species to their habitat. In this study, we employed a systematic survey design to quantify the temporal variability in the marine-bird community and relate it to the physical oceanography of the northeastern Chukchi Sea. The objectives of this study were to (1) describe seasonal, spatial, and interannual variation in the distribution, abundance, and community composition of marine birds; (2) describe seasonal, spatial, and interannual variation in physical oceanography; and (3) explore relationships between the abundance of 8 marine-bird species and the hydrographic structure of their habitat.

2. Study area

In the Chukchi Sea, the net flow of water is northward through Bering Strait and toward the Arctic Ocean (Coachman et al., 1975). The broad northward flow through Bering Strait is steered by bathymetry into three main branches—one east of Hanna Shoal that feeds into Barrow Canyon, one west of Herald Shoal that feeds into Herald Valley, and one between the two shoals, referred to as the Central Channel flow (Fig. 1; Weingartner et al., 1998,2005). This separation also is evident in water-mass properties (Woodgate et al., 2005). Within the Chukchi Sea, the Alaska Coastal Current (ACC) lies east near the Alaska coastline and flows northward, carrying Alaskan Coastal Water (ACW), a warm (>2 °C), low-salinity (<32.2) water mass that originates south of Bering Strait. The currents farther offshore move Bering Sea Water (BSW; Coachman et al., 1975), a warm (>2 °C), high-salinity (>32.4) water mass, northward through the Central Channel and Herald Valley (Weingartner et al., 2005). This BSW is a mixture of Anadyr Water and Bering Shelf Water from south of Bering Strait, so it has a higher nutrient content and transports greater numbers of oceanic zooplankton than does ACW (Walsh et al., 1989; Springer and McRoy, 1993).

In addition to these water masses that are advected northward, water in the Chukchi Sea is modified during the fall and winter by ice formation and during the spring by ice melt. As is the case with ACW, cold (-1 to $+2$ °C), low-salinity (<30) Meltwater (MW) is depleted of nutrients and large oceanic zooplankton. In the summer, the bottom half of the water column usually still contains cold (-2 to $+1$ °C), salty (>32) Winter Water (WW) left over from the previous winter, whereas the surface layer consists of either MW or BSW. This stratification increases from spring to summer and typically erodes in the fall as strong winds, cooling, and freezing enhance vertical mixing (Weingartner et al., 2005).

This study was conducted in the northeastern Chukchi Sea, in a region extending ~110–180 km west of the village of Wainwright, off of the northwestern coast of Alaska and included 3 study areas that are of interest for oil and gas exploration: Klondike, Burger, and Statoil (Fig. 1). The Klondike study area was located on the eastern side of the Central Channel and nearest the inflow of BSW, whereas the Burger study area was located to the northeast of Klondike and on the southern slope of Hanna Shoal. The Statoil study area was located to the north of both Klondike and Burger; its western edge was near to the Central Channel and its eastern half lay on the southern slope of Hanna Shoal. The ACC flows east of all 3 study areas, exiting the area via Barrow Canyon, whereas the Central Channel flow passes over or just west of Klondike and Statoil.

3. Methods

3.1. Data collection

We conducted research cruises during 3 seasons in 2008–2010 that covered the entire open-water period of the northeastern Chukchi Sea (Fig. 2): late summer (hereafter "Jul/Aug"), early fall (hereafter "Aug/Sep"), and late fall (hereafter "Sep/Oct"). The Klondike and Burger study areas consisted of boxes that were ~56 km on a side (Fig. 1). The Statoil box was configured to encompass several Statoil oil-lease blocks and had the same total area as Klondike and Burger. These ~3000-km^2 study-area boxes were the primary focus of all sampling. We conducted line-transect surveys for birds along a series of parallel survey lines that ran north–south through the study areas. The sampling grid included lines on the eastern and western boundaries of each study area and lines spaced ~1.8 km apart within each study area, creating a set of 31 parallel survey lines in Klondike and Burger that were ~56 km long each. Because the Statoil box was not square, its survey lines were of variable length, ranging from 42 to 56 km. We surveyed continuously when the ship was moving along a straight-line course at a minimal velocity of 9.3 km h^{-1} (5 kt; Tasker et al., 1984; Gould and Forsell, 1989) and recorded environmental conditions every 10 min. We collected data 9–12 h day^{-1} during daylight hours, weather and ice conditions permitting. We generally stopped surveys when sea height was Beaufort 6 (seas ~2–3 m) or higher, although we occasionally continued to sample if observation conditions were still acceptable (e.g., if seas were at the lower end of Beaufort 6 and we were traveling with the wind and seas). One observer stationed on the bridge of the vessel recorded all birds seen within a radius of 300 m in a 90° arc from the bow to the beam on

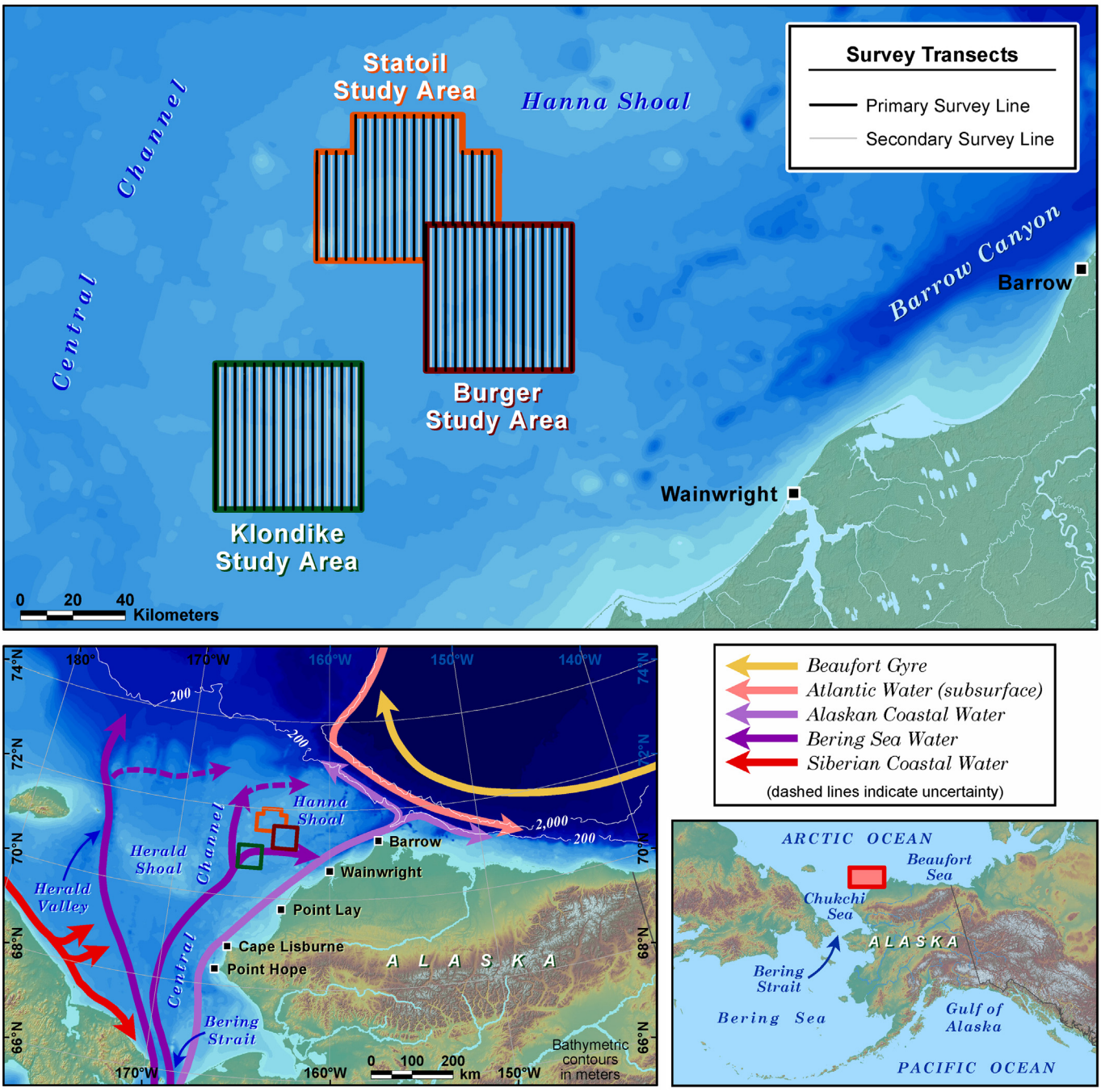

Fig. 1. Northeastern Chukchi Sea, Alaska, showing main oceanographic features and study-area boxes.

one side of the ship (the count zone), locating and identifying seabirds with 10X binoculars as needed. For each bird or group of birds, we recorded species, total number of individuals; distance from the observer when sighted (in 50-m bins), and radial angle of the observation from the bow of the ship.

In the count zone, we counted all birds on the water, taking care to avoid recounting the same individuals. For flying birds, however, we conducted scans for them $\sim$1 time min^{-1} (the exact frequency varied with ship's speed) and recorded an instantaneous count (or "snapshot") of all birds flying within the count zone. The snapshot method reduces the bias of overestimating the density of flying birds (Tasker et al., 1984; Gould and Forsell, 1989). We counted only those flying birds that entered the count zone from the sides or front and excluded flying birds that entered from behind the ship (i.e., an area that already had been surveyed) to avoid the possibility of counting ship-following birds.

We entered all data directly into a computer connected to a global positioning system (GPS) with DLog software (R. G. Ford Consulting, Portland, OR) in 2008 and TigerObserver software (TigerSoft, Las Vegas, NV) in 2009 and 2010. These programs time-stamped and geo-referenced every observation.

Within each study-area box, we surveyed the hydrography at a series of 25 stations that were fixed in a grid with $\sim$13.8-km (7.5-NM) spacing. We collected data with a Seabird SBE-19+V2 CTD sampling at 4 Hz that was lowered through the water-column at a rate of $\sim$0.5 m s^{-1}. Measured variables included pressure, temperature, and conductivity, which then were converted to depth, temperature ($\pm$0.005 °C), and salinity ($\pm$0.02).

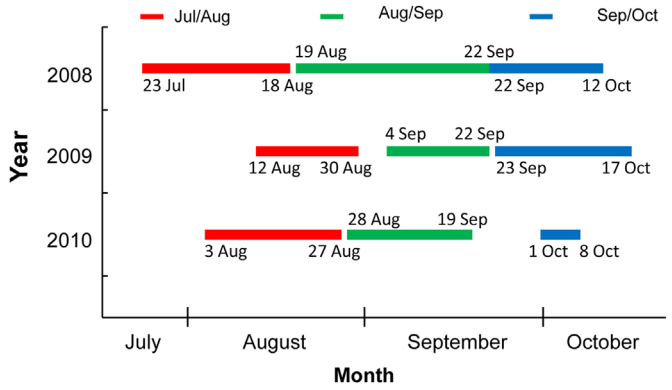

Fig. 2. Timing of boat-based surveys for marine birds in the northeastern Chukchi Sea, 2008–2010.

3.2. Data analyses

3.2.1. Marine-bird distribution and abundance

We analyzed trends in the seasonal distribution and abundance of a suite of 8 ecologically diverse species that represented a variety of prey preferences and foraging methods, thereby providing a comprehensive view of the seabird community as a whole. We estimated corrected densities (birds km^{-2}) within each study area by using line-transect sampling analyses available in the program DISTANCE 6.0 Release 2 (Thomas et al., 2010) and followed analytical methods described by Buckland et al. (2001,2004). This approach accounts for the decrease in probability of detecting a bird with increased distance from the survey line. These corrected density estimates were calculated with the formula:

$$\hat{D} = \frac{n \cdot \hat{E}(s)}{L \cdot \hat{P}_c}$$

where $\hat{D}$ is the corrected density estimate, n is the total number of observations seen on transects, $\hat{E}(s)$ is the mean flock size, L is the total length of survey lines sampled, and $\hat{P}_c$ is the probability of detection estimated by the model (Buckland et al., 2001).

Each focal species had >350 observations total, which provided enough data to model the probability of detection with confidence. We pooled species of similar size, conformation, and detection probability into detection groups as follows: small alcids (crested auklets, least auklets), light-colored large birds (black-legged kittiwakes, glaucous gulls [*Larus hyperboreus*], northern fulmars [*Fulmarus glacialis*]), and phalaropes (red-necked [*Phalaropus lobatus*] and red [*P. fulicarius*] phalaropes, which are difficult to distinguish during this period and are treated hereafter collectively). We modeled detection functions for short-tailed shearwaters and thick-billed murres individually because preliminary examination of the perpendicular-distance histograms suggested that their respective detection probabilities were different from those of other focal species. All shearwaters identified were short-tailed shearwaters; in addition, no other *Puffinus* spp. are known to occur north of Bering Strait (Kessel and Gibson, 1978).

We calculated perpendicular sighting distances from the radial angle of observation and the maximal value of the corresponding detection-distance bin after truncating all data at 250 m, following procedures recommended by Buckland et al. (2001). For each detection group, we fitted models that used 1 of 2 possible key functions (half-normal or hazard-rate) to the distribution of perpendicular distances to find the model that best estimated the probability of detection. We included covariates in the model sets to account for possible differences in detection among observation platforms (i.e., vessel), observers, and sea-surface conditions (measured on the Beaufort scale). The fit of each model was assessed with Akaike's Information Criterion (AIC), diagnostic plots, and a Kolmogorov–Smirnov goodness-of-fit test (following Buckland et al., 2004). For each detection group, we regressed log (observed flock size) against estimated detection probability to test for "size bias" (i.e. the tendency to observe more large flocks at large distances). In all cases, the regression slope was not significantly different from zero ($P > 0.10$), so we used mean observed flock size as an estimate of $\hat{E}(s)$.

Once a detection model was selected for a detection group (Table 1), we calculated species-specific corrected density estimates by running separate analyses that filtered for each species and then applied the group detection probability to the uncorrected estimates. We calculated corrected densities of each species by study area, season, and year. We calculated variances with the delta method and calculated log-normal, z-based, two-sided 95% confidence intervals for the estimates of density with equations 3.71–3.74 in Buckland et al. (2001). This method assumed that encounter-rate estimates were independent of detection probabilities among years, seasons, and study areas and pooled estimates of $\hat{P}_c$ and $\hat{E}(s)$ by covariates.

We used ANOVAs to examine differences in bird densities between the Klondike and Burger study areas, among seasons, and among years for each species. We examined the seasonal trend in bird densities at Statoil in 2010 but did not include Statoil in the ANOVA analysis because it was surveyed only twice and only in 2010. We report mean values with 95% confidence interval (CI) unless otherwise stated. In all statistical tests, the level of significance (α) was 0.05. All distance sampling and ANOVA analyses were conducted with the statistical software R 2.13.0 (http://www.r-project.org).

We also used the geo-located observations to generate maps of distribution and abundance for individual species of interest. First, we assigned the density value of each transect to its respective transect centroid coordinate. We then used the inverse-distance-weighted (IDW) interpolation technique of the Spatial Analyst extension of ArcMap GIS software (Environmental Systems Research Institute, Inc., Redlands, CA) to generate contours of similar density, based on the mean density for each grid-cell centroid. To conduct the IDW analysis, we first overlaid a 1000×1000-m^2 grid over the study area. The IDW interpolation technique calculated the distance-weighted mean density of up to 9 centroids within 7000 m of each 1000-m pixel in the study area. This analysis

Table 1
Detection function model parameters used to calculate corrected densities by taxon.

Species	Function shape	Covariates	Probability of detection (flock)	CV (%)	Mean flock size
Crested Auklet	Half-normal	Observer+vessel	0.66	1.3	4.3
Least Auklet					1.8
Black-legged Kittiwake	Half-normal	Observer	0.58	2.1	1.7
Glaucous Gull					1.2
Northern Fulmar					1.4
Red Phalarope	Half-normal	None	0.52	4.2	4.2
Red-necked Phalarope					
Short-tailed Shearwater	Half-normal	Observer+vessel	0.71	1.9	4.9
Thick-billed Murre	Hazard-rate	None	0.82	1.9	1.7

produced contoured portrayals of bird densities on maps within each of the 3 study areas.

3.2.2. Seabird community analysis

For the analysis of community composition, we included all bird observations that were identified at least to family. We summarized seabird species-composition by study area, season, and year (Magurran, 2004). We aggregated individual species into 6 taxonomic species-groups prior to analysis to simplify the interpretation and presentation of results: waterfowl (family Anatidae, including geese, swans, and ducks), loons (family Gaviidae), tubenoses (family Procellariidae, including fulmars and shearwaters), phalaropes (shorebirds of the family Scolopacidae that spend most of their lives on the ocean), larids (families Laridae and Stercorariidae, including gulls, terns, and jaegers), and alcids (family Alcidae, including murres, dovekies [*Alle alle*], guillemots, murrelets, auklets, and puffins).

We used multivariate analyses and descriptive statistics to explore seasonal and interannual changes in the structure of the seabird community. We grouped the data into sample units by study area, season, and year, then used ordination for analysis of the 2008–2010 seabird data from all study areas. We used the taxonomic species-groups to calculate a Bray–Curtis similarity matrix (Bray and Curtis, 1957) to which we applied non-metric multidimensional scaling (MDS; Clarke and Green, 1988). This ordination technique visualizes the similarity in community composition among samples as distances mapped in 2-dimensional space (Clarke and Green, 1988). Finally, we determined the dominant species assemblages composing each sample. The MDS analysis was conducted with the package 'vegan' (Oksanen et al., 2011) in R.

3.2.3. Physical oceanography

We processed data from CTD downcasts according to the manufacturer's recommended procedures (SBE Data Processing manual) and further screened for anomalous spikes, dropouts, and density inversions. We averaged data from the vertical profiles to 1 dbar ($\sim$1 m) to examine seasonal and interannual variations in the characteristics and distribution of water masses over our study areas. For each survey, we plotted CTD data as vertical sections along transects that extend from southwest to northeast and across the Klondike and Burger study areas. These transects were selected because they compose the broadest possible coverage from the survey cruises in all 3 years. We also examined plots of salinity and temperature averaged over the mixed layer and contoured by latitude and longitude to compare Klondike, Burger, and Statoil.

3.2.4. Habitat associations

We used generalized linear models (GLMs) to examine the relationship between hydrography and seabird abundance for each of the 8 focal species. We quantified the structure of the water column with 4 explanatory variables: depth of the mixed layer (meters), strength of stratification (calculated as the maximal value of change in density m^{-1} $[\delta\rho/\delta z]$), average temperature of the mixed layer, and average salinity of the mixed layer (Fig. 3). These values were averaged from 25 fixed stations within each study area in each season and year.

Models were specified as negative binomial with a log-link to meet the assumptions of normality and account for overdispersion in the data (Zuur et al., 2009). We examined the correlation coefficients and variance inflation factors (VIF) of the explanatory variables for collinearity (Zuur et al., 2009). All correlation coefficients were <0.50, and all VIF were <3, indicating no collinearity. We assessed model adequacy with plots of residuals, normal probability, and Cook's distance.

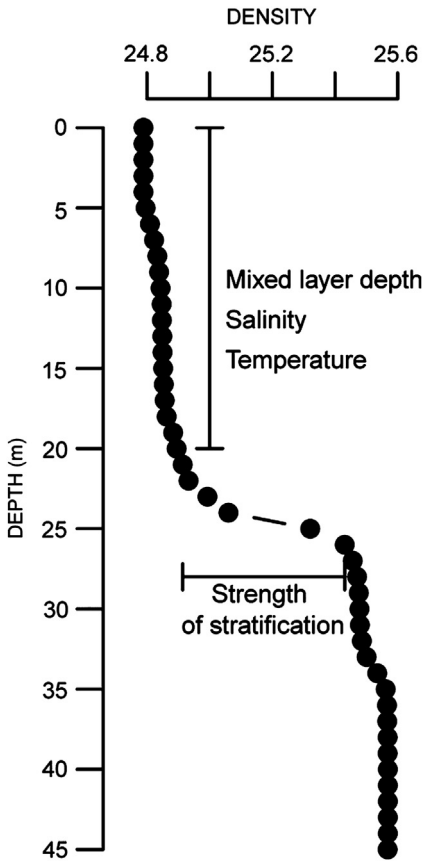

Fig. 3. Depth profile illustrating the oceanographic variables used to quantify habitat characteristics.

We constructed a model set for each species that included all possible additive combinations of the 4 oceanographic variables that describe the characteristics of water-masses in this region (Table 2). We also included a model specifying constant abundance to confirm that significant variation in abundance was explained by the other models in the candidate set. All models included an offset term of log (effective area surveyed [i.e., transect length $\times$ transect width $\times \hat{P}_c$]) to account for survey effort and the species-specific probability of detection (Hedley et al., 2004). Models were weighted based on the difference between each model's AIC_c value and that of the top-ranked model, and the weights were normalized to sum to 1 over all models considered (Burnham and Anderson, 2002). The model with the lowest AIC_c value was selected as the best approximating model given the data, and models within 2 AIC_c units of the top-ranked model were considered well supported by the data for drawing inferences (Burnham and Anderson, 2002). We used model-averaged estimates from the candidate model set ($\Delta AIC_c \leq 2$) to draw inference about variation in seabird abundance. Model-averaged estimates and unconditional standard errors account for model selection uncertainty (Burnham and Anderson, 2002). All GLM analyses were conducted with the package MASS (Venables and Ripley, 2002) in R.

4. Results

4.1. Marine-bird distribution and abundance

Seabirds were more abundant overall in 2009 than they were in 2008 or 2010 (Table 3). In 2008, we estimated a total of 80,200 birds (95% CI: 68,300–94,300 birds) of 31 species during all

Table 2
Candidate models to relate seabird abundance to oceanographic variables during the open-water seasons 2008–2010 in the northeastern Chukchi Sea. In this table, *n* represents counts, MLD is the mixed-layer depth, and eff. area is an offset included in all models that accounts for survey effort and detection probability.

Habitat factors	Models
Null	$n \sim 1 +$ eff. area
Depth of stratification	$n \sim$ MLD + eff. area
Temperature of foraging habitat	$n \sim$ temperature + eff. area
Salinity of foraging habitat	$n \sim$ salinity + eff. area
Strength of stratification	$n \sim$ stratification + eff. area
Salinity and thickness of the mixed layer	$n \sim$ MLD + temperature + eff. area
Temperature and thickness of the mixed layer	$n \sim$ MLD + salinity + eff. area
Water-column structure	$n \sim$ MLD + stratification + eff. area
Temperature and water-column structure	$n \sim$ MLD + temperature + stratification + eff. area
Salinity and water-column structure	$n \sim$ MLD + salinity + stratification + eff. area
Water-mass characteristics only	$n \sim$ temperature + salinity + eff. area
All mixed-layer characteristics	$n \sim$ MLD + temperature + salinity + stratification + eff. area

Table 3
Estimated abundance of seabirds counted during boat-based marine surveys in the northeastern Chukchi Sea, by study area, year, and season. Values in parentheses are 95% confidence intervals.

Year/season	Study area			Total
	Klondike	Burger	Statoil	
2008				
Jul/Aug	8400	1000	–	9400
	(5900–11,900)	(700–1400)	–	(6800–12,900)
Aug/Sep	18 800	127,300	–	30,400
	(14,300–24,900)	(100,900–160,600)	–	(24,400–37,700)
Sep/Oct	26,500	22,500	–	40,500
	(17,100–40,800)	(14,200–35,700)	–	(31,100–52,800)
2009				
Jul/Aug	17,200	13,200	–	146,100
	(13,200–22,300)	(9200–18,900)	–	(119,000–179,600)
Aug/Sep	214,800	109,300	–	324,100
	(171,700–268,700)	(83,300–143,400)	–	(272,100–386,000)
Sep/Oct	44,500	37,400	–	67,600
	(37,300–53,200)	(31,100–45,100)	–	(49,500–92,400)
2010				
Jul/Aug	33,300	7200	20,400	69,400
	(24,400–45,500)	(5000–10,300)	(15,000–27,700)	(54,400–88,400)
Aug/Sep	60,400	7300	42,100	124,100
	(42,600–85,500)	(5500–9500)	(35,200–50,400)	(111,800–137,800)
Sep/Oct	–	23,800	–	23,800
	–	(18,400–30,800)	–	(18,400–30,800)

surveys combined. In 2009, we estimated a total of 537,800 birds (95% CI: 474,300–609,900 birds) of 24 species during all surveys combined. In 2010, we added the Statoil study area and estimated a total of 217,300 birds (95% CI: 196,200–240,600 birds) of 29 species during all surveys combined.

4.1.1. *Planktivorous birds*

Crested auklets were the most abundant species recorded in all 3 years of the study (Fig. 4). Densities differed significantly among seasons and between study areas in all 3 years ($P < 0.001$ for STUDY AREA × SEASON × YEAR). Crested auklets were more abundant in Klondike than in Burger in 2008, more abundant in Burger than in Klondike in 2009, and not significantly different among study areas in 2010 (Fig. 4). Least auklet densities also differed significantly between study areas and among seasons in all 3 years ($P < 0.001$ for STUDY AREA × SEASON × YEAR). Densities of least auklets were higher in Klondike than in Burger in all 3 seasons of 2008, but there was no consistent trend in other years (Fig. 4). Phalarope densities differed significantly between study areas and among seasons in all 3 years ($P < 0.001$ for STUDY AREA × SEASON × YEAR). Phalaropes were seen in patchy, dispersed feeding flocks, primarily in Aug/Sep and Sep/Oct in 2008, in Jul/Aug and Aug/Sep in 2009, and in Aug/Sep in 2010 (Fig. 4).

4.1.2. *Piscivorous birds*

Black-legged kittiwake densities differed significantly between study areas and among seasons ($P < 0.001$ for STUDY AREA × SEASON). They were distributed widely, occurring in both study areas and in all 3 seasons during 2008 and 2009 (Fig. 5). In 2010, Black-legged kittiwakes occurred in all 3 study areas in Jul/Aug and Aug/Sep but were absent from Burger in Sep/Oct (Fig. 5). Thick-billed murre densities were consistently higher in Klondike than in Burger and were the lowest in Sep/Oct in all years ($P < 0.001$ for STUDY AREA and SEASON; Fig. 5). In 2010, densities of thick-billed murres in Burger and Statoil were lower than densities in Klondike and followed a similar seasonal pattern of decline from Jul/Aug onward; densities in Burger approached zero in Sept/Oct.

4.1.3. *Omnivorous birds*

Short-tailed shearwaters were the second-most-abundant species in all 3 years of the study. Their densities differed significantly

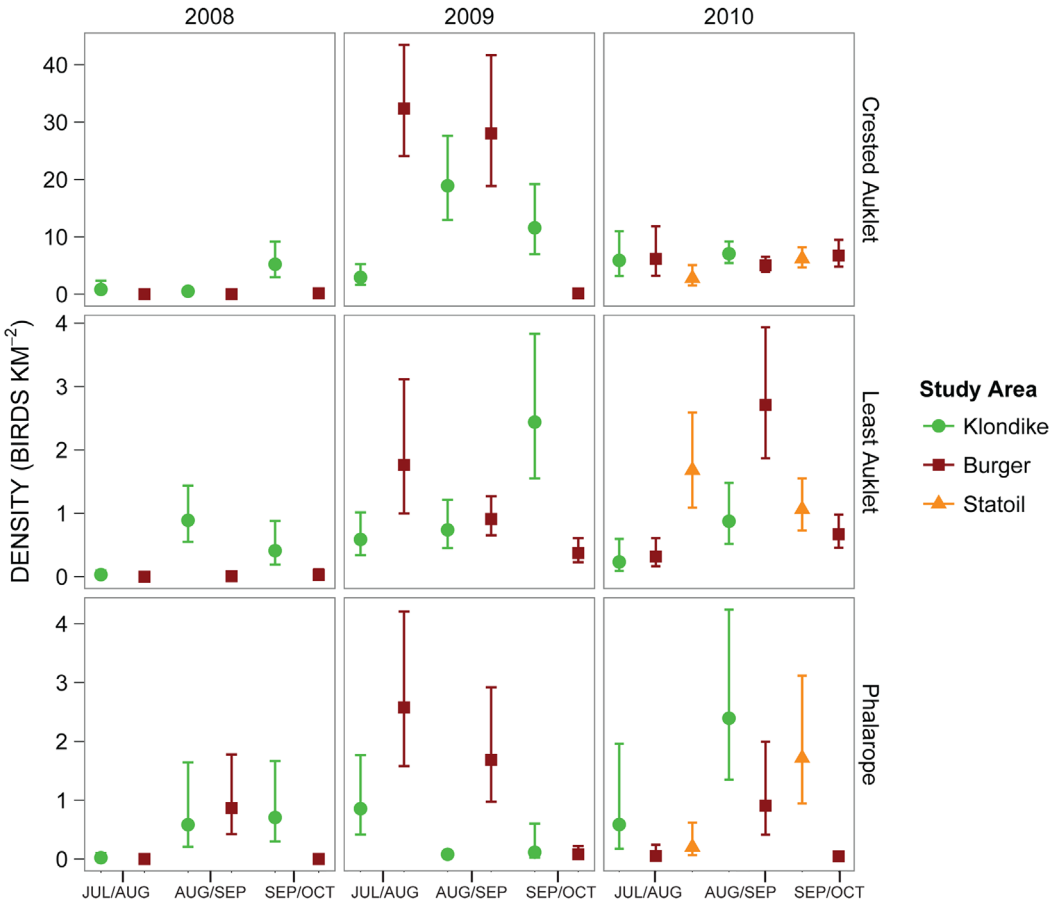

Fig. 4. Mean density (birds km^{-2}) of crested auklets, least auklets, and phalaropes on transect in the Klondike, Burger, and Statoil study areas in 2008–2010, by study area and season. Error bars represent 95% confidence intervals. Range of values on the *y*-axis differs among species.

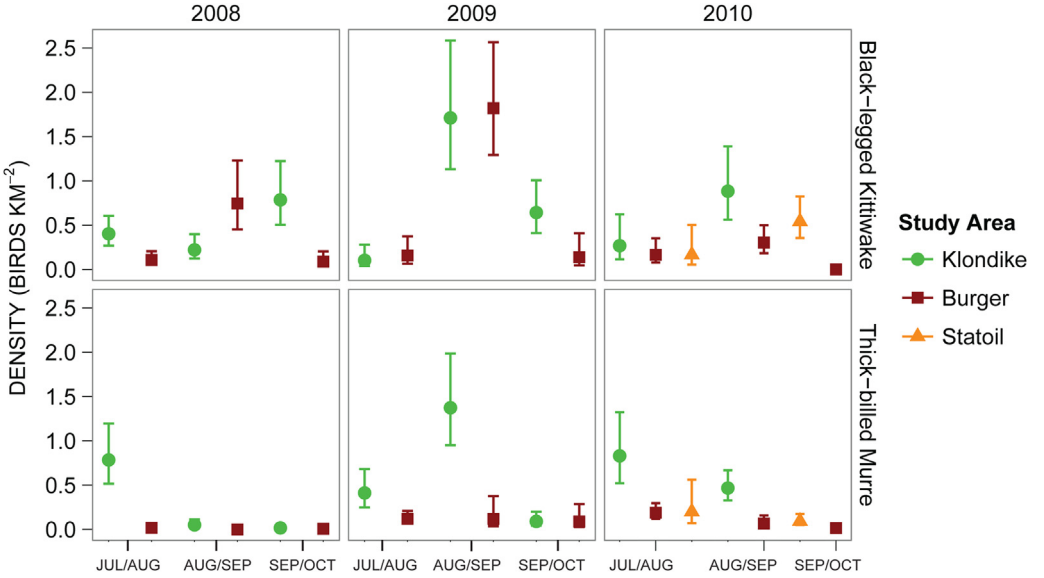

Fig. 5. Mean density (birds km^{-2}) of black-legged kittiwakes and thick-billed murres on transect in the Klondike, Burger, and Statoil study areas in 2008–2010, by study area and season. Error bars represent 95% confidence intervals.

between study areas and among seasons in all 3 years ($P < 0.001$ for STUDY AREA × SEASON × YEAR). They generally were more abundant in Klondike than in Burger in 2008 and 2009 but were not significantly different among study areas in 2010 (Fig. 6). In all years, short-tailed shearwaters were most abundant in Aug/Sep (Fig. 6). Northern fulmar densities varied among seasons and years ($P < 0.001$ for SEASON × YEAR). They were significantly more abundant in Klondike than in Burger in 2008 (Fig. 6), but densities did not differ significantly among study areas in 2009 or 2010. Glaucous gull densities differed significantly among study areas, seasons, and years ($P \leq 0.01$ for STUDY AREA × SEASON × YEAR). Like short-tailed shearwaters, they also were widespread,

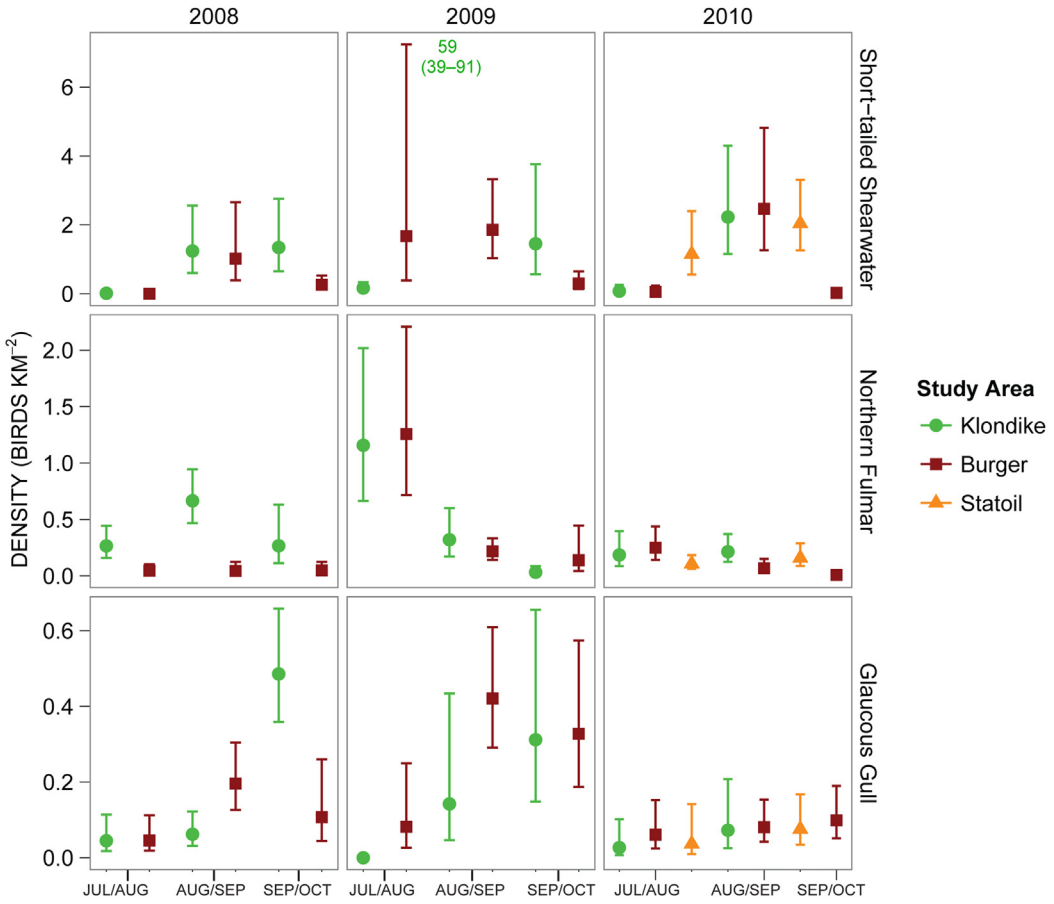

Fig. 6. Mean density (birds km^{-2}) of short-tailed shearwaters, northern fulmars, and glaucous gulls on transect in the Klondike, Burger, and Statoil study areas in 2008–2010, by study area and season. Error bars represent 95% confidence intervals. Range of values on the *y*-axis differs among species and one value for short-tailed shearwaters beyond the range of the axes is presented in text on the figure.

occurring in all study areas and in all seasons surveyed except for Klondike in Jul/Aug 2009 (Fig. 6).

4.2. Community analysis

We recorded a total of 34 species in these study areas during 2008–2010 (Appendix A). Multivariate analyses of the seabird community indicated that species composition varied primarily among years and showed a consistent pattern of seasonal change. The MDS ordination separated into 3 groups, with some overlap (misclassification) of study areas by season and year (Fig. 7). The stress coefficient of the ordination was 0.09, indicating a good fit to the data (Clarke and Ainsworth, 1993). Samples from 2008 and 2010 represented distinct groups with little overlap (Fig. 7A). In contrast, 2009 overlapped both of the other years in Jul/Aug and Sep/Oct but showed a distinct community structure in Aug/Sep. When the points in the MDS ordination were grouped by season, there was a shift in community composition from Jul/Aug to Aug/Sep; then, the community structure shifted back toward the Jul/Aug structure in Sep/Oct (Fig. 7B). Much of this pattern was driven by the extreme seasonal changes in species composition in Burger during 2008 (Fig. 8).

The patterns in species composition identified in the multivariate analyses were reflected in changes in the relative abundance of each of the 6 species-groups among study areas, seasons, and years (Fig. 8). Most notably, the relative abundance of alcids in all study areas combined increased from 2008 to 2010. Klondike was dominated numerically by alcids (primarily crested auklets) and tubenoses (primarily short-tailed shearwaters) in all years. Burger was dominated numerically by larids (primarily black-legged kittiwakes) and tubenoses in 2008, but alcids were most abundant in 2009. In 2010, alcids were the most abundant species-group in all 3 study areas and in all seasons, composing 65–88% of all birds. Waterfowl and loons were the least common species-groups and consisted primarily of flocks of long-tailed ducks (*Clangula hyemalis*) and pacific loons (*Gavia pacifica*), respectively.

4.3. Physical oceanography

In all years, warm, moderately saline Bering Sea Water (BSW) flowed northward into the vicinity of the study areas, gradually replacing the cold, saline Winter Water (WW) formed during the previous winter and sharing the surface layer with cold, fresh Meltwater (MW; Figs. 9 and 10). This WW was representative of the entire water column during the winter and was modified in the upper layer during the spring and summer by ice melt and advection. The timing and extent of the advection, as indicated by increases in the temperature (Fig. 9) and salinity (Fig. 10) of the upper mixed layer, varied among study areas and years. In all years, the salinity and temperature were higher over Klondike than over Burger, indicating that BSW always was present. In contrast, MW was present over Burger in all years, although its spatial extent varied widely among years (extensive in 2008, restricted to the northeastern corner in 2009, and restricted to the northeastern half in 2010).

The interannual variation in marine habitat characteristics was most apparent during Aug/Sep. In 2008, temperatures in the

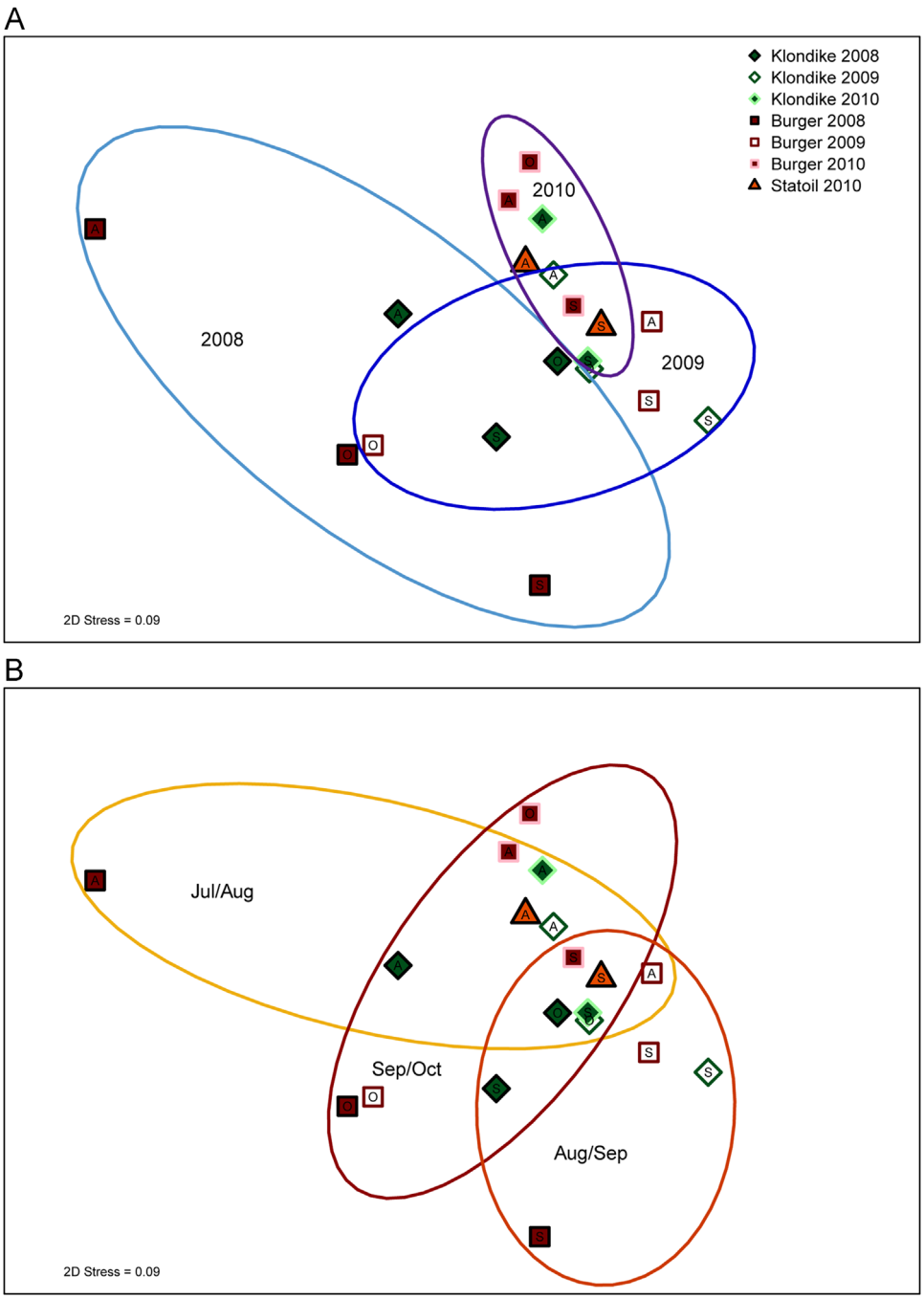

Fig. 7. Non-metric multidimensional scaling ordination plot of Bray–Curtis similarities for density of seabirds recorded in the northeastern Chukchi Sea during 2008–2010, where distance between samples represents similarity in composition. Samples are grouped by year (A) and by season (B).

upper mixed layer ranged from 3.5 °C on the western edge of Klondike to 0–2 °C over Burger, with a front clearly visible between the two study areas (Fig. 9; top row, middle panel). In 2009, the mixed layer was nearly homogenous across both study areas, with a slight decrease in temperature from 5.5 °C to 4.5 °C (Fig. 9, middle row, middle panel) and a gradual decrease in salinity from 31.5 to 30 from the southwestern corner of Klondike to the northeastern corner of Burger (Fig. 10, middle row, middle panel). In 2010, temperatures over Klondike (6–8 °C) were twice those over Burger (3–4 °C), with values in Statoil spanning the range between the other 2 study areas (3–6 °C; Fig. 9, bottom row, middle panel).

Vertical sections of density indicate that the strength and depth of stratification varied considerably among years and study areas (Fig. 11). Stratification was strong throughout 2008 and moderate in 2010, with the pycnocline at ~20–25 m. In 2009, the pycnocline was weaker and deeper (~30 m) than in the other years. Klondike was consistently less stratified than Burger (Fig. 11), because Burger contained more low-salinity MW in the upper half of the water column and more high-salinity WW in the lower water column than Klondike did.

4.4. Habitat associations

Alcids (3 species), phalaropes, and northern fulmars were associated with distinct oceanographic habitats (Fig. 12). The best-fitting models for these 5 taxa included strength of stratification, and models for 4 of these taxa also included average

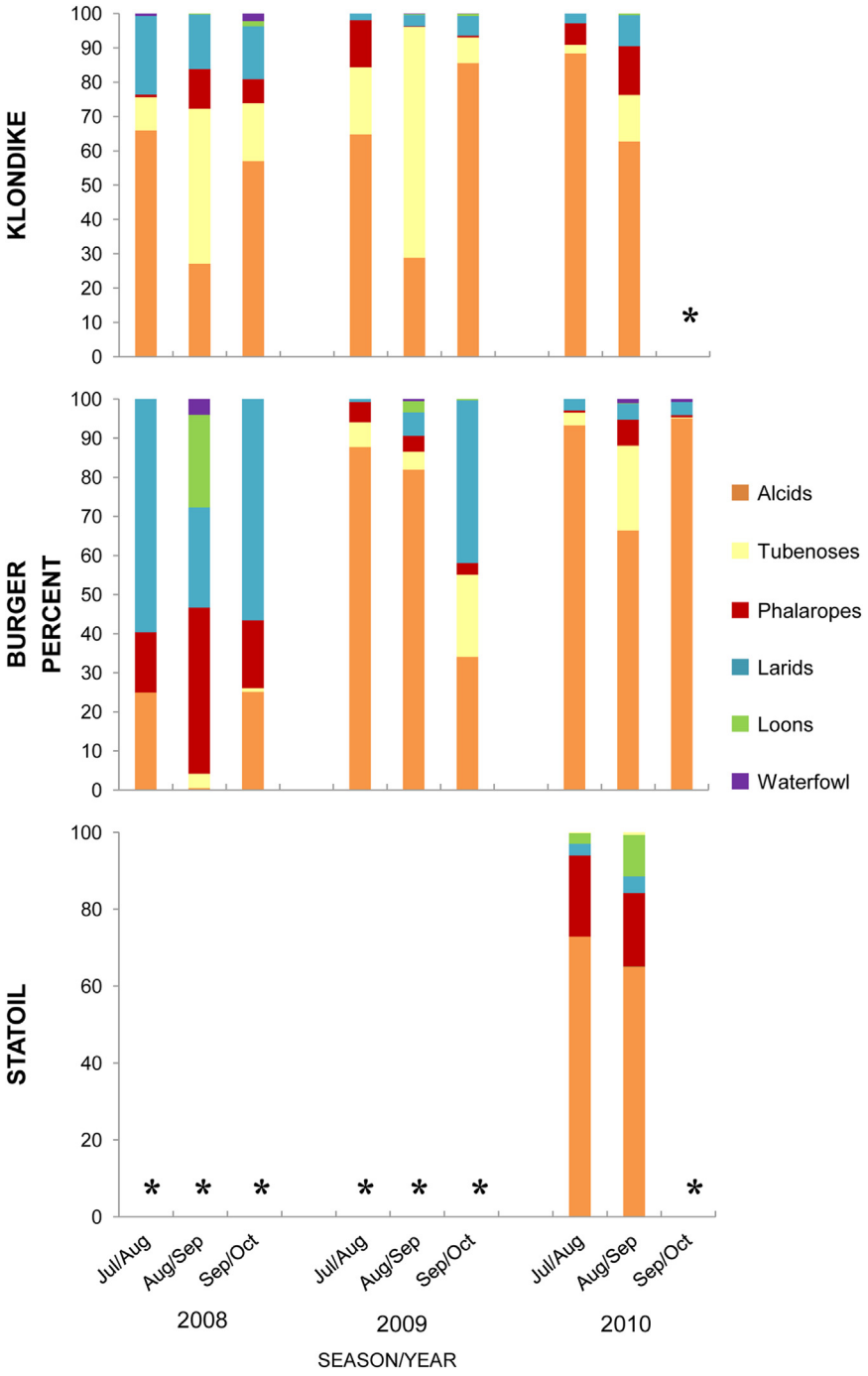

Fig. 8. Species-composition of the seabird community on transect in the Klondike, Burger, and Statoil study areas, by season and year. Asterisks indicate no data.

salinity of the upper mixed layer (Table 4). The best-fitting models for crested auklets and thick-billed murres also included average temperature of the mixed layer. In all cases, the parameter values in the best-fitting models were significantly different from zero. The best-fitting models for these 5 taxa also included mixed-layer depth, but the parameter estimates were not significantly different from zero, indicating that this variable was not a strong predictor of seabird abundance. The best-fitting models for short-tailed shearwaters, black-legged kittiwakes, and glaucous gulls, indicated that none of the environmental variables significantly explained variation in abundance of these species.

Due to the uncertainty in model selection, we relied on model-averaged parameter estimates and confidence intervals to draw inferences about the relationship between each environmental variable and seabird abundance (Burnham and Anderson, 2002). Strength of stratification was the best predictor of abundance for 5 of the taxa (Fig. 12). Least auklets, crested auklets, thick-billed murres, and northern fulmars were positively associated with strength of stratification, whereas phalaropes were negatively associated with it (Fig. 12). Salinity was positively associated with the abundance of 4 taxa: least auklets, crested auklets, phalaropes, and northern fulmars. Temperature was positively associated with the abundance of thick-billed murres. The depth

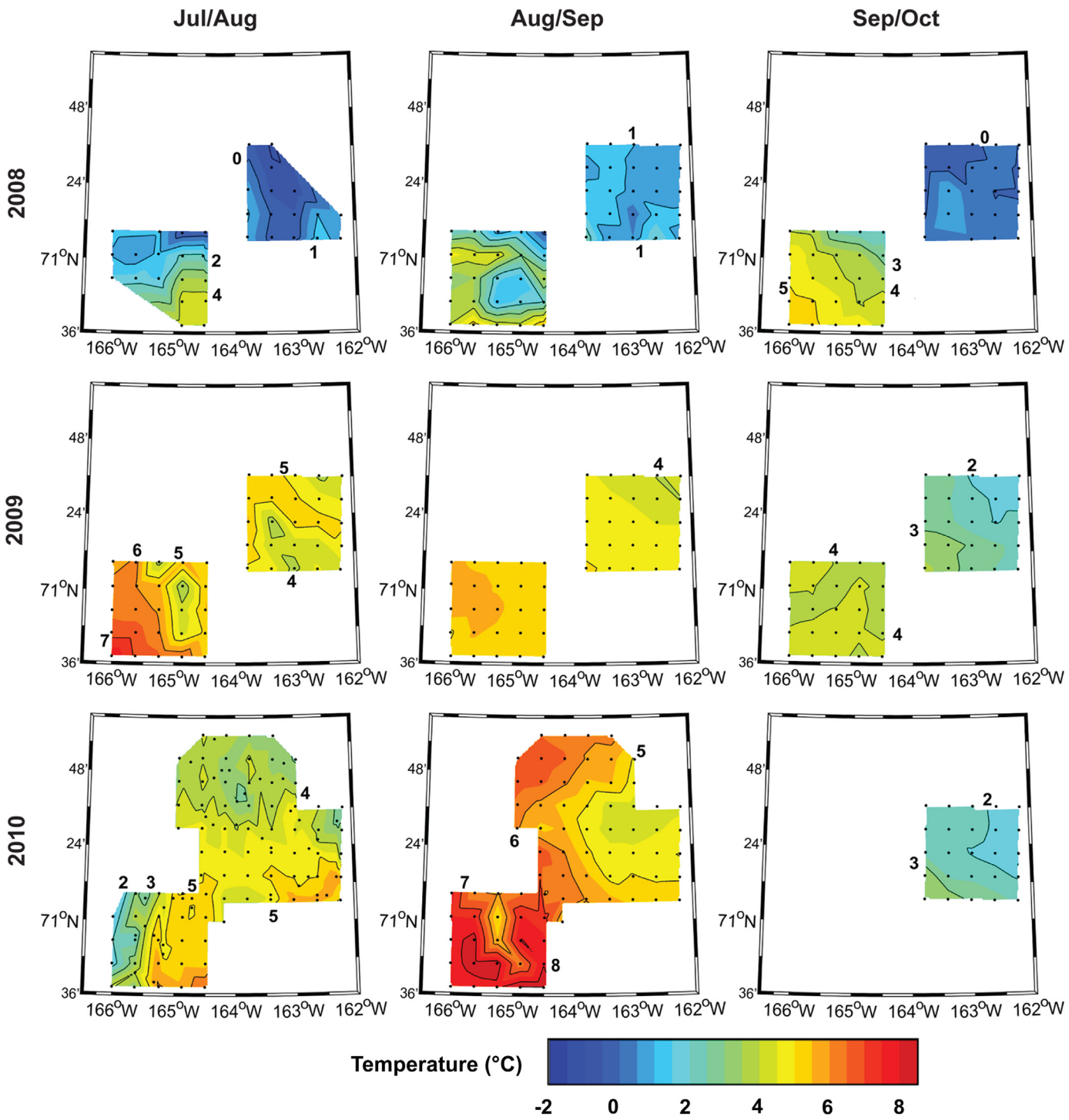

Fig. 9. Plan view of temperatures averaged over the upper 10 m of the water column for surveys conducted in the northeastern Chukchi Sea during Jul/Aug, Aug/Sep, and Sep/Oct, 2008–2010. Klondike is in the lower left, Burger is on the right, and Statoil (2010 only) is above and left of Burger.

of the mixed layer was not associated with the abundance of any species.

5. Discussion

5.1. Bering Sea Water boundary region

We propose here that the oceanography differs among the 3 study areas seasonally and interannually (see also Weingartner et al., 2013) and that these differences create spatial and temporal differences in the structure of the seabird community in the northeastern Chukchi Sea. The movement of oceanic water northward from through Bering Strait influences the patterns of productivity throughout the Chukchi Sea (Grebmeier et al., 2006). In-situ primary production in the Bering Sea Water (BSW) near Bering Strait is on the order of $\sim$470 g C m^{-2} yr^{-1}, whereas production in the northern Chukchi Sea generally is on the order of $\sim$80 g C m^{-2} yr^{-1} (Sambrotto et al., 1984; Hansell et al., 1989, Hill et al., 2005). The BSW also advects large oceanic

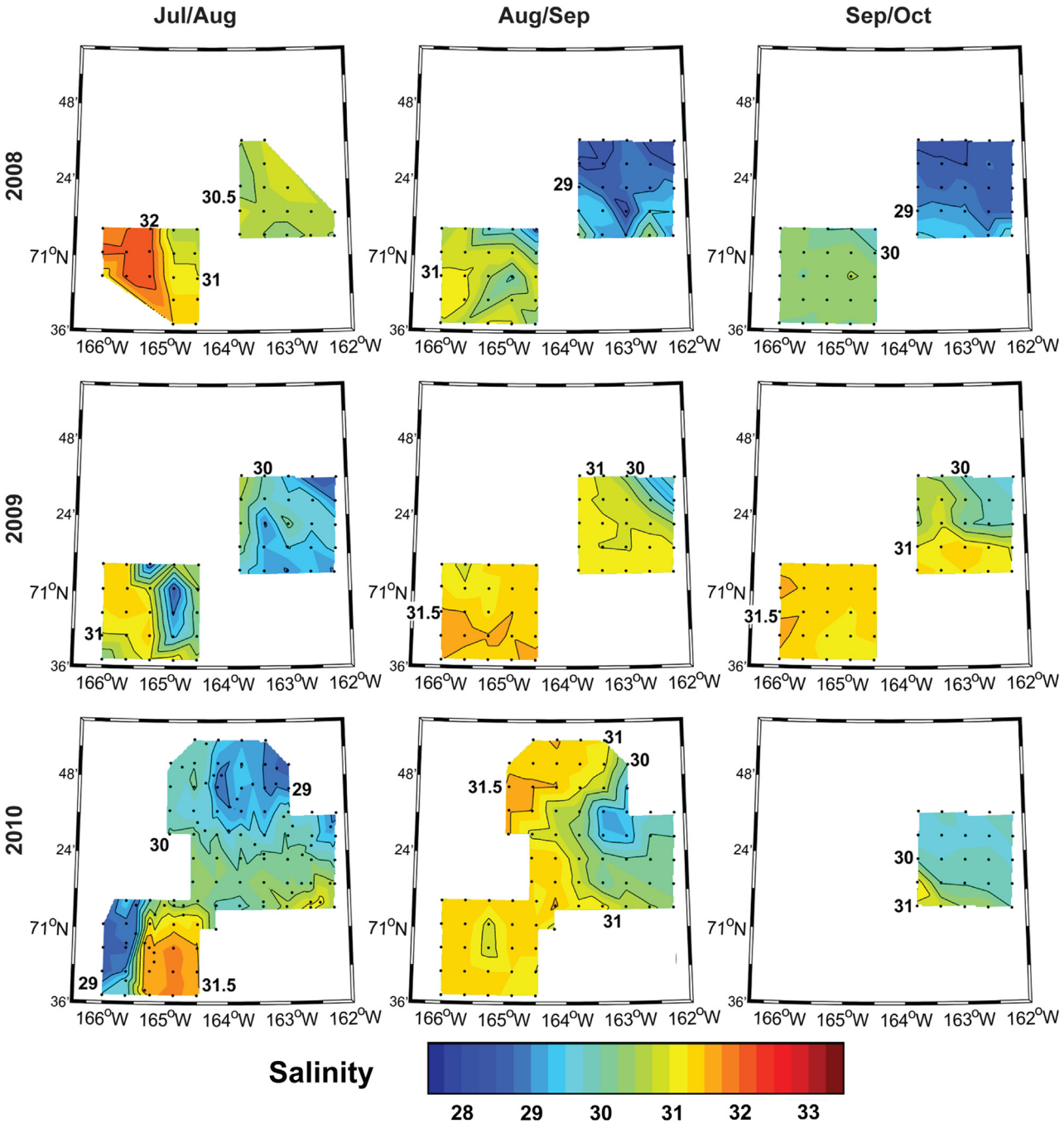

Fig. 10. Plan view of salinities averaged over the upper 10 m of the water column for surveys conducted in the northeastern Chukchi Sea during Jul/Aug, Aug/Sep, and Sep/Oct, 2008–2010. Klondike is in the lower left, Burger is on the right, and Statoil (2010 only) is above and left of Burger.

zooplankton into the area from the Bering Sea Basin (Grebmeier et al., 2006), and these large zooplankton can graze much of the phytoplankton when they are present. In contrast, shelf zooplankton associated with resident waters do not significantly graze much of the primary production, which falls to the bottom and nourishes a high-biomass, diverse benthic community (Feder et al., 1994; Grebmeier et al., 2006; Blanchard et al., 2013a, 2013b).

In the southern Chukchi Sea, an oceanographic front between BSW and Alaskan Coastal Water (ACW) is the defining feature that separates distinct benthic communities (Grebmeier et al., 2006; Bluhm et al., 2009), with higher biomass and bivalve abundance under BSW and lower biomass under ACW. In our study areas, communities also are structured by processes associated with a front at times, but the water masses involved are different from those found farther south. Despite the shallow bathymetry, our study areas straddle a region that resembles the interface found at a shelf break in that there is a transition from a stream of oceanic water entrained in the Central Channel to a 2-layer water column with little transport trapped over Hanna Shoal.

In terms of the fate of primary production, Klondike appears to be a pelagic-dominated system and Burger appears to be a benthic-dominated system, with the transition between the 2 systems falling between the 2 study areas (Day et al., 2013). This transition zone is seen clearly in Statoil, which was added to the study in 2010 and spans the longitudes between Klondike and Burger. The gradient in community structure is oriented east–west at the mesoscale of these study areas (10 s–100 s km), rather than north–south and is consistent with observations from the

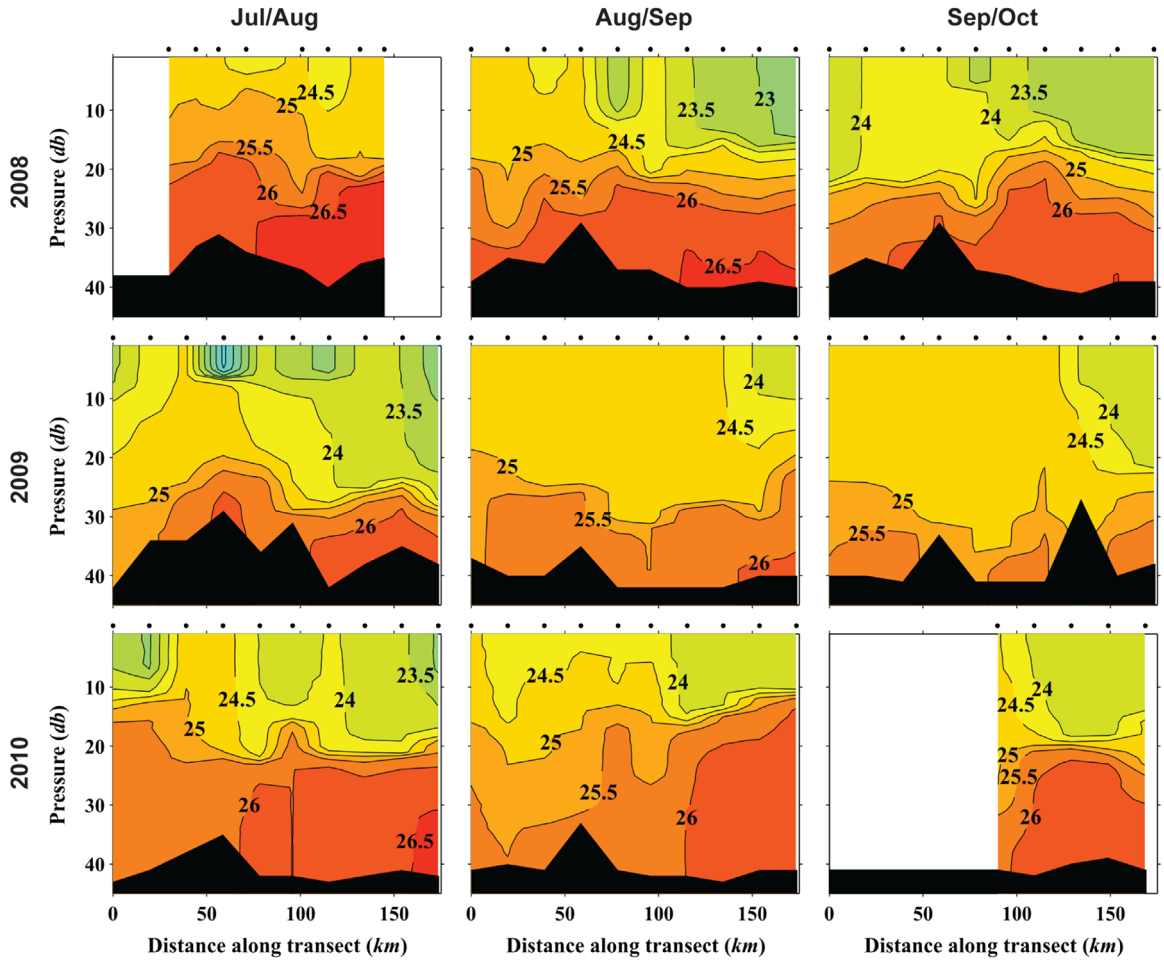

Fig. 11. Vertical sections of density from the southwest corner of Klondike to the northeast corner of Burger in the northeastern Chukchi Sea during Jul/Aug, Aug/Sep, and Sep/Oct, 2008–2010.

southern Chukchi Sea (Piatt and Springer, 2003; Grebmeier et al., 2006). As evident in the plots of temperature and salinity, the Central Channel flow was visible along the western edge of the Klondike study area throughout the open-water season of 2008, and much of that study area was dominated by its associated water mass—BSW. In contrast, the surface of Burger had no strong current flow and was dominated by Meltwater at the surface and Winter Water on the bottom (i.e., it functioned more as shelf or coastal water than as oceanic water). This oceanographic boundary between the 2 study areas shifted to the northeast in 2010, a warmer year when the pack ice retreated almost entirely before the start of our sampling. In that year, the water-column structure indicated that BSW dominated the upper mixed layer in Klondike in Jul/Aug and expanded toward the northeast, into Burger and Statoil, in Aug/Sep. These oceanographic distinctions between the Klondike and Burger study areas were least apparent in 2009, the warmest year of the study, when the water-column was essentially BSW down to 30 m and across most of both study areas (Weingartner et al., 2013). In that year, the boundary between water advected that summer and water modified during the preceding winter was located in the northeastern corner of the Burger study area when we began sampling in early August.

5.2. *Variations in marine-bird abundance and community structure*

The distribution of seabirds, particularly the planktivorous species, is influenced in the northeastern Chukchi Sea by advective processes that transport oceanic species of zooplankton from the Bering Sea. Planktivorous seabirds are most abundant in areas where their prey is concentrated within 20 m of the surface (Hunt et al., 1990; Haney, 1991; Piatt and Springer, 2003), so they are responsive to conditions that make their prey both abundant and accessible. Total seabird abundance was the highest in 2009, the lowest in 2008, and intermediate in 2010 (Table 3); and this variation reflected changes in the location and strength of the boundary between BSW and MW (Figs. 9 and 10), although the connections to zooplankton populations appeared less clear (Questel et al., 2013). The year of lowest total seabird abundance (2008) was associated with the coldest overall water temperatures, weak stratification, late inflow of BSW that did not develop until Sep/Oct, and the lowest biomass of large zooplankton. The year of highest total seabird abundance (2009) was associated with the strongest and earliest intrusion of warm BSW into the study region, but it was accompanied by only intermediate biomass of large zooplankton. The warm BSW established vertical stratification of the water-column in Jul/Aug that persisted until Sep/Oct. Both planktivorous and piscivorous seabird species prefer to forage in areas where the water-column is stratified, concentrating prey (Piatt and Springer, 2003); foraging conditions in 2009 were ideal for these marine predators. The year of intermediate seabird abundance (2010) was associated with later intrusion of BSW, later establishment of stratification during Aug/Sep, and the highest biomass of large zooplankton (e.g., large calanoid copepods and euphausiids). Based on the limited sampling conducted in Burger in Sep/Oct, it appears that the stratification weakened, but persisted; this persistent stratification was reflected in the persistence of substantial numbers of

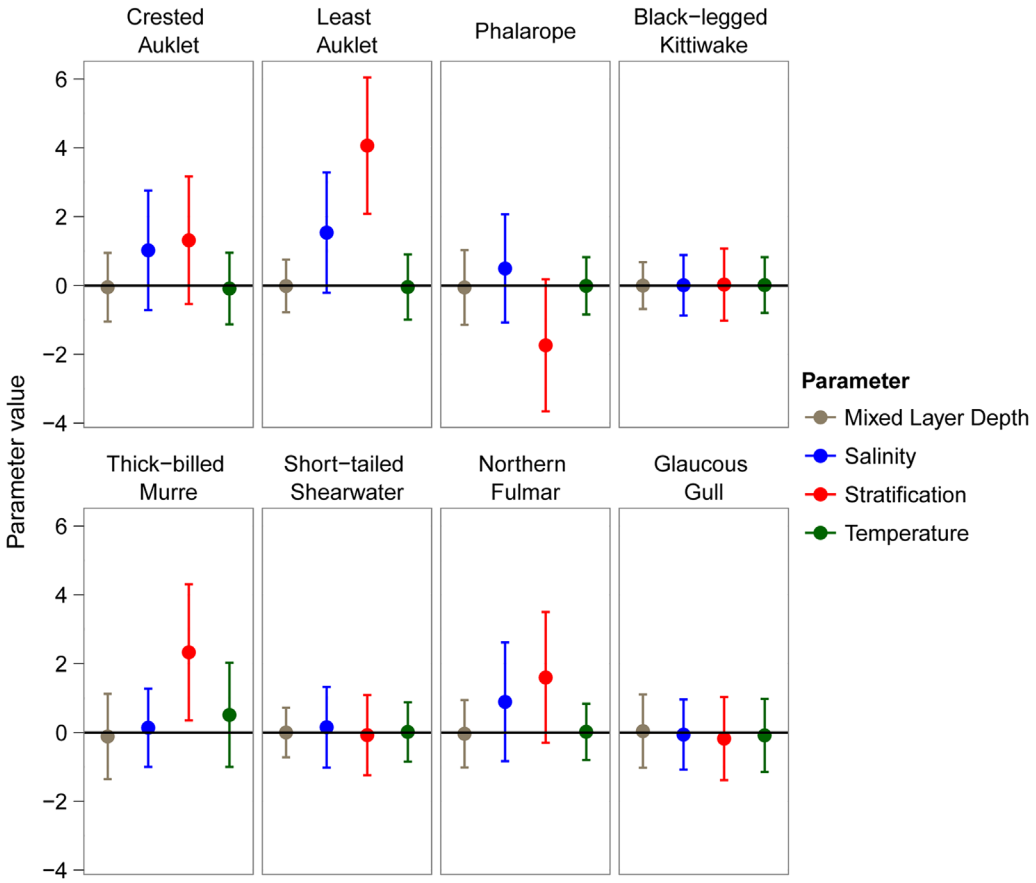

Fig. 12. Model-averaged parameter estimates and unconditional confidence intervals that indicate the relationship between oceanographic characteristics and seabird abundance for 8 taxa in the northeastern Chukchi Sea. Parameter values are on log-scale because a log-link was used in the models to satisfy the assumptions of linear models.

seabirds in the study area. We unfortunately lack information on the vertical distribution of zooplankton to explore these interactions further; consequently, we can only speculate on the mechanisms.

In addition to changes in total abundance, the community composition changed among seasons and years. This seasonal shift is partially dictated by the development of open water. As the ice retreats and foraging habitat becomes available, species move in from foraging areas to the south and from terrestrial breeding areas. Of the colonial seabirds, thick-billed murres, common murres (*U. aalge*), and black-legged kittiwakes nest in large numbers on cliffs along the Chukchi coast as far north as Cape Lisburne and are common offshore during Jul/Aug and Aug/Sep (Divoky, 1987; Kuletz et al., 2008). Species that nest on the tundra, such as phalaropes and jaegers, move out to sea in Aug/Sep and join millions of short-tailed shearwaters that migrate from their breeding grounds in Australia to forage in the Northern Hemisphere during the austral winter (Baduini et al., 2001). Finally, ice-associated gulls such as Ross's gulls (*Rhodostethia rosea*) and ivory gulls (*Pagophila eburnea*) migrate from high-arctic breeding areas in Russia and Canada into the Chukchi Sea as the ice advances southward in the late fall.

The seasonal pattern in species-composition was similar from year to year, with the numerical dominance shifting from primarily alcids in Jul/Aug (except for Burger in 2008) to a mix of auklets, shearwaters, and phalaropes (all of which are primarily zooplankton-feeders) in Aug/Sep, then shifting back toward the initial composition in Sep/Oct. The same differences in community composition occurred among years, with 2008 (and especially the Burger study area) distinct from the other 2 years, primarily because of the low densities of alcids in that year. Densities of diving species such as alcids and short-tailed shearwaters fluctuated by four orders of magnitude among years, whereas the variation in the density of surface-feeding gulls among years was only one order of magnitude. This fairly consistent contribution from larids among years indicates that most of the variation in the seabird community can be attributed to birds that are primarily planktivorous.

5.2.1. *Planktivorous seabirds*

The distribution and abundance of individual species of planktivorous seabirds demonstrates the relationship between foraging ecology and foraging habitat as defined by physical oceanography. Crested auklets consume primarily euphausiids (e.g., *Thysanoessa* spp.) and large copepods (e.g., *Neocalanus cristatus*, *Eucalanus bungii*) characteristic of oceanic water (Bédard, 1969; Kitaysky and Golubova, 2000; Gall et al., 2006). Least auklets consume both oceanic and neritic copepods (e.g., *Calanus marshallae*; Hunt et al., 1998; Gall et al., 2006). Crested auklets typically forage at depths up to 25 m (Hunt et al., 1998), whereas, least auklets' small size (~90 g) and physiology restrict their diving to the upper 10–15 m of the water-column (Hunt, 1997). Both of these species rely on internal waves to push pycnoclines towards the surface, concentrating prey within their foraging depth (Haney, 1991; Hunt et al., 1998). South of Bering Strait, these species occur near fronts between oceanic Anadyr Water and Bering Shelf Water and in stratified water if the upper mixed layer is the Bering Shelf Water (Elphick and Hunt, 1993; Hunt, 1997). Our habitat models indicate that the abundance of crested and least auklets was positively associated with stratification, a hydrographic feature that concentrates prey

Table 4
Model selection results from the effects of oceanographic variables on abundance of 8 taxa of seabirds. We present models within 2 AICc units of the top-ranked model, the variables included in each model, the difference in adjusted Akaike's information criterion between the top-ranked model and other candidate models (ΔAIC_c), and the AIC_c weight for each model.

Species/Taxon	Formula	AIC_c	ΔAIC_c	Weight
Least Auklet	$n \sim$ stratification + salinity + eff. area	199.59	0.00	0.45
	$n \sim$ temperature + salinity + stratification + eff. area	200.98	1.39	0.22
	$n \sim$ MLD + salinity + stratification + eff. area	201.31	1.72	0.19
	$n \sim$ MLD + temperature + salinity + stratification + eff. area	202.28	2.69	0.12
Crested Auklet	$n \sim$ MLD + temperature + salinity + stratification + eff. area	286.57	0.00	0.15
	$n \sim$ stratification + salinity + eff. area	287.03	0.46	0.12
	$n \sim$ salinity + eff. area	287.26	0.69	0.11
	$n \sim 1$ + eff. area	287.73	1.16	0.09
	$n \sim$ MLD + salinity + eff. area	287.81	1.24	0.08
	$n \sim$ temperature + salinity + stratification + eff. area	288.01	1.44	0.07
	$n \sim$ temperature + salinity + eff. area	288.66	2.09	0.05
Thick-billed Murre	$n \sim$ MLD + temperature + stratification + eff. area	164.22	0.00	0.46
	$n \sim$ MLD + temperature + salinity + stratification + eff. area	165.23	1.01	0.28
Northern Fulmar	$n \sim$ MLD + salinity + stratification + eff. area	173.07	0.00	0.26
	$n \sim$ stratification + salinity + eff. area	173.11	0.03	0.26
	$n \sim$ MLD + salinity + eff. area	174.79	1.72	0.11
	$n \sim$ MLD + temperature + salinity + stratification + eff. area	174.86	1.79	0.11
	$n \sim$ temperature + salinity + stratification + eff. area	174.95	1.87	0.10
Phalaropes	$n \sim$ MLD + salinity + stratification + eff. area	187.96	0.00	0.26
	$n \sim$ MLD + temperature + salinity + stratification + eff. area	189.61	1.64	0.11
	$n \sim$ stratification + eff. area	189.76	1.80	0.11
	$n \sim$ MLD + salinity + eff. area	189.83	1.87	0.10
	$n \sim$ stratification + salinity + eff. area	189.96	2.00	0.09
Glaucous Gull	$n \sim$ MLD + temperature + eff. area	145.85	0.00	0.18
	$n \sim$ MLD + eff. area	146.57	0.73	0.13
	$n \sim 1$ + eff. area	146.77	0.93	0.11
	$n \sim$ MLD + salinity + eff. area	147.14	1.29	0.10
	$n \sim$ temperature + eff. area	147.63	1.78	0.07
	$n \sim$ MLD + temperature + stratification + eff. area	147.69	1.84	0.07
Black-legged Kittiwake	$n \sim 1$ + eff. area	192.26	0.00	0.28
	$n \sim$ temperature + eff. area	194.06	1.79	0.11
	$n \sim$ salinity + eff. area	194.23	1.97	0.10
	$n \sim$ stratification + eff. area	194.25	1.98	0.10
	$n \sim$ MLD + eff. area	194.26	2.00	0.10
Short-tailed Shearwater	$n \sim 1$ + eff. area	208.12	0.00	0.21
	$n \sim$ salinity + eff. area	208.72	0.60	0.16
	$n \sim$ temperature + eff. area	209.60	1.48	0.10
	$n \sim$ MLD + eff. area	209.90	1.78	0.09
	$n \sim$ stratification + eff. area	209.93	1.81	0.09

within the water-column (Elphick and Hunt, 1993; Hunt, 1997), and salinity, an indicator of the presence of BSW. The spatial patterns of crested auklet distribution varied among seasons and years, suggesting that the birds were responding to interannual variations in their habitat (Fig. 13). In 2008, their distribution was similar to the distribution of BSW and highest in Klondike, whereas, in 2009 and 2010, years when BSW extended over more of the study areas, crested auklets were found in high abundance throughout all of the study areas (Fig. 13). Oceanographic characteristics associated with crested and least auklets in the northeastern Chukchi Sea are consistent with habitat that maximizes the abundance and accessibility of oceanic copepods.

The distribution and abundance of planktivorous species that feed at or near the surface also reflected their respective foraging strategies. Phalaropes have the most restricted foraging habitat of the planktivorous species we studied; they forage only on the surface and typically are associated with microscale divergence and convergence fronts that concentrate prey within ~0.2 m of the surface (Brown and Gaskin, 1988). Unlike least and crested auklets, the abundance of phalaropes was negatively associated with stratification. Additionally, their distribution was highly clumped, and they were particularly abundant when and where there were filaments of cold water at or near the surface (e.g., Klondike in Aug/Sep 2008, Burger in Jul/Aug 2009).

5.2.2. *Piscivorous seabirds*

The variation in distribution and abundance of piscivorous species, as indicated by black-legged kittiwakes and thick-billed murres, is probably related to the difference in foraging strategies between these two species. Despite being classified as piscivorous (Piatt and Springer, 2003), black-legged kittiwakes are surface-feeding gulls that will consume both fishes and larger zooplankton (Hobson, 1993; Jodice et al., 2006; Iverson et al., 2007), and thick-billed murres are diving alcids that will consume both fishes and large invertebrates (Woo et al., 2008). Thick-billed murres occurred almost exclusively in Klondike in all years and disappeared by Sep/Oct of each year. Their abundance was positively associated with stratification, suggesting that they had very restricted foraging habitat that was located primarily in BSW. Black-legged kittiwakes were not associated with any of the oceanographic variables that we examined. They had a consistent seasonal pattern of abundance in Burger in all years, but densities in Klondike tended to be the highest when BSW

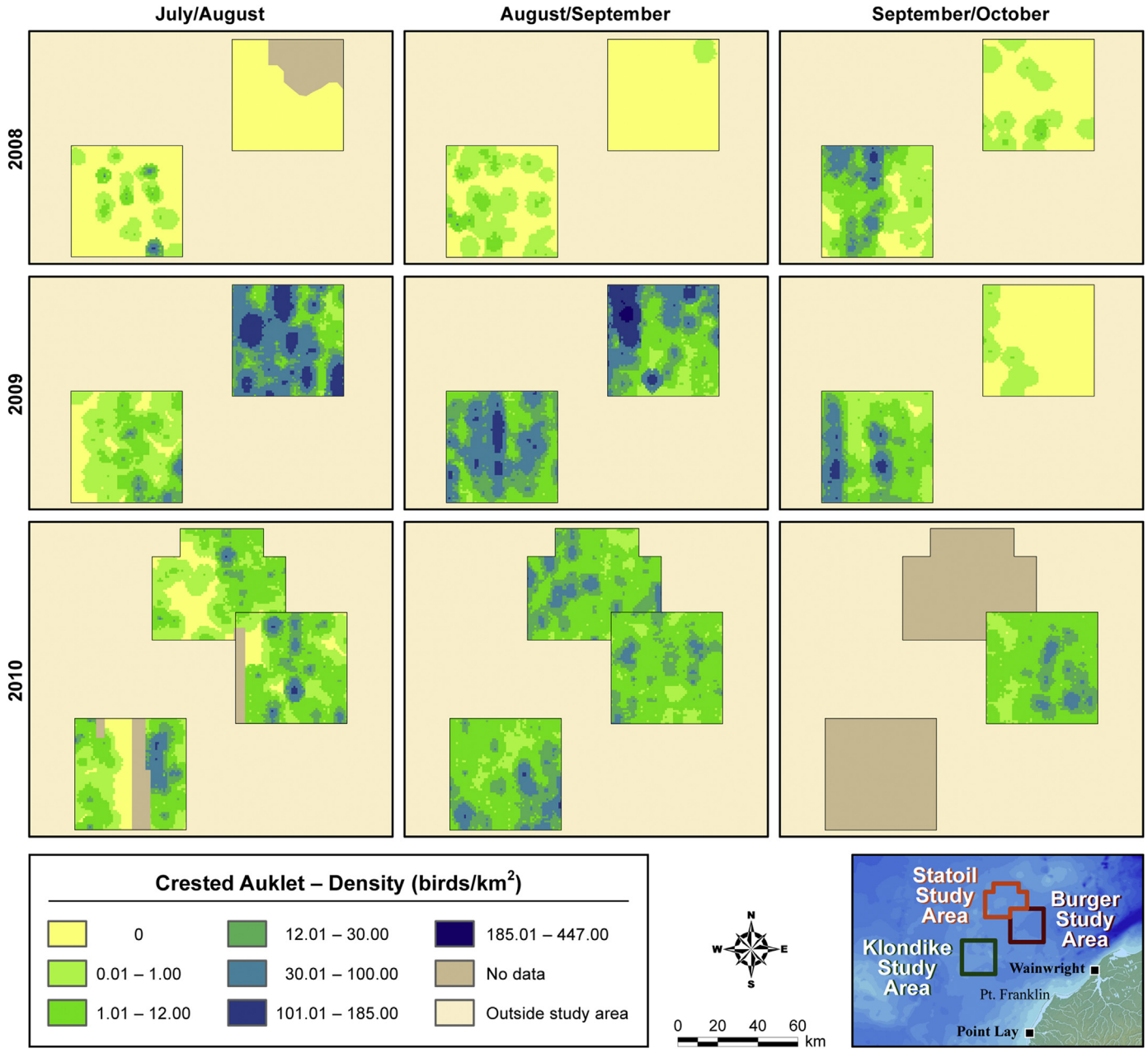

Fig. 13. Distribution of estimated densities (birds km^{-2}) of crested auklets recorded on transect in the Klondike, Burger, and Statoil study areas of the northeastern Chukchi Sea in 2008–2010, by season and year.

occupied more of Klondike than it did of Burger (Fig. 14), suggesting that black-legged kittiwakes were foraging on prey species associated with BSW but may be less restricted in their foraging requirements than are thick-billed murres. These results are consistent with patterns observed in the southeastern Bering Sea, where black-legged kittiwakes were found to be widespread foragers, whereas thick-billed murres foraged close to their breeding colonies (Sigler et al., 2012).

5.2.3. Omnivorous seabirds

The distribution of short-tailed shearwaters did not appear tightly coupled with particular features of the water-column. Short-tailed shearwaters are fairly large seabirds that consume a variety of large zooplankton, in addition to fish and squid (Hunt et al., 2002; Jahncke et al., 2005) and can dive as deep as 70 m to forage (Weimerskirch and Cherel, 1998). The magnitude of interannual variation in the abundance of short-tailed shearwaters during this study was similar to that of primarily planktivorous seabirds, but their seasonal pattern of abundance was consistent among years (i.e., always highest in Aug/Sep; Fig. 15), suggesting that they are responding to oceanographic structure at a broader spatial scale than what was sampled in this study.

The distribution and abundance of the other omnivorous species, as characterized by northern fulmars and glaucous gulls, reflected their flexibility in foraging behavior. Both species were present in low densities in all 3 years—densities considerably lower than the high, but variable, densities of planktivorous species—and both were most abundant in 2009, least abundant in 2010, and intermediate in abundance in 2008. Like the planktivorous seabirds, northern fulmars were positively associated with salinity and stratification, perhaps indicating a greater reliance on zooplankton than the generalist short-tailed shearwaters and glaucous gulls; however, they were less abundant in 2010 than in 2008, which was the year of lowest alcid

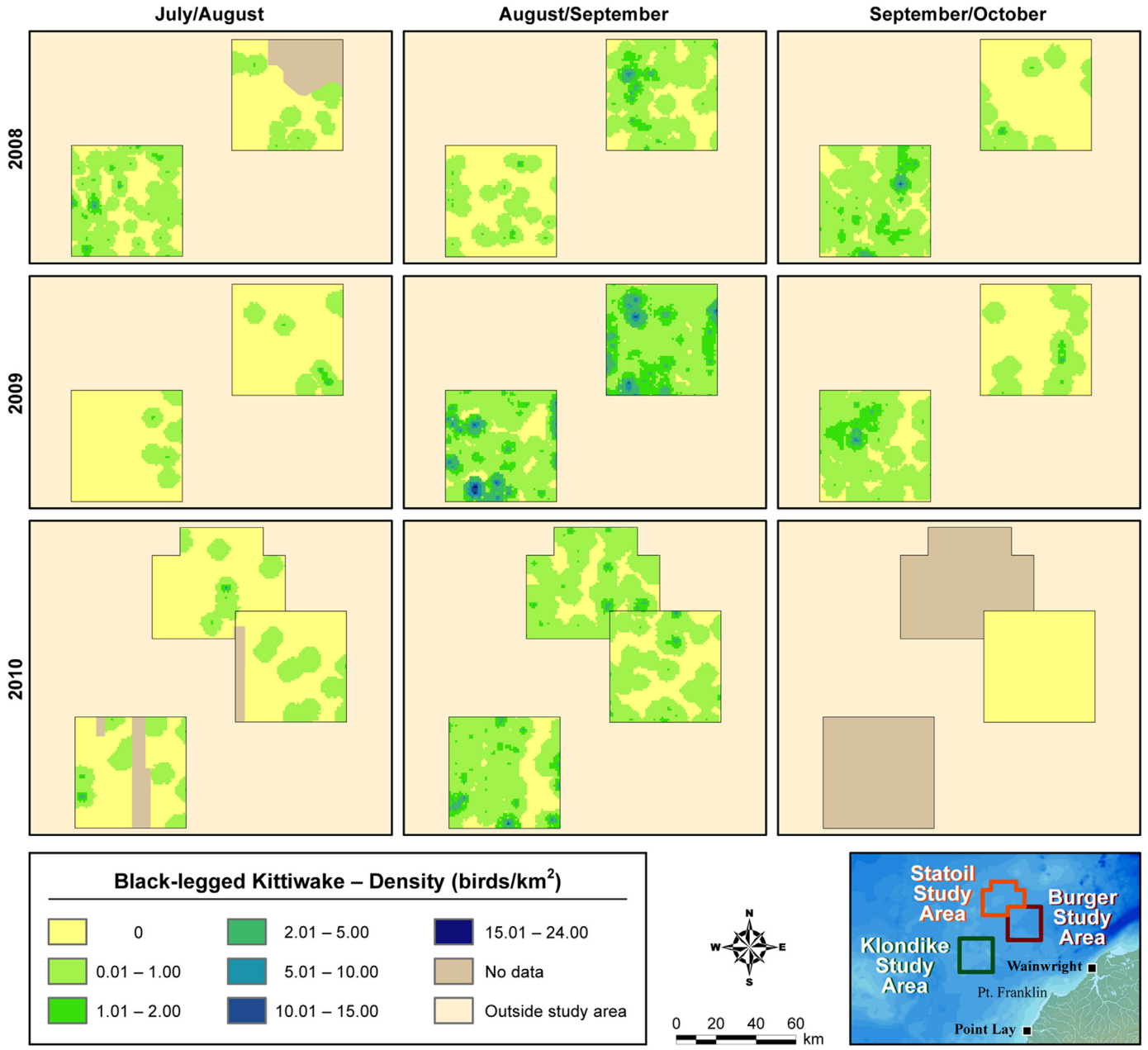

Fig. 14. Distribution of estimated densities (birds km^{-2}) of black-legged kittiwakes recorded on transect in the Klondike, Burger, and Statoil study areas of the northeastern Chukchi Sea in 2008–2010, by season and year.

and phalarope abundance. Glaucous gulls were the least abundant of the 8 focal species in our study and showed a consistent seasonal pattern of increasing abundance from Jul/Aug to Sep/Oct in all years. They had no apparent association with oceanographic variables at the scale of the study areas.

5.2.4. *Rare species*

The presence and absence of species among years also demonstrates the influence of physical oceanography on seabird community structure. In 2008, when water temperatures remained cold until late in the open-water season, we observed ice-associated species such as ivory gulls (*Pagophila eburnea*) and black guillemots (*Cepphus grille*). In 2009, when water temperatures were warm for most of the open-water season, we did not see the ice-associated species, migrating waterfowl (e.g., king eiders [*Somateria spectabilis*], common eiders [*S. mollissima*]), migrating waterbirds (e.g., red-throated loons [*Gavia stellata*]), or species that would be considered at the edge of their range (e.g., dovekies, pigeon guillemots [*Cepphus columba*]); these species were recorded only in 2008 and/or 2010.

Perhaps the most curious presence of a rare species outside of its range was the appearance of Ancient Murrelets (*Synthliboramphus antiquus*) in all 3 study areas in Aug/Sep 2010 and lingering in Klondike and Burger into Sep/Oct 2010. The closest known breeding populations of this small, nocturnal alcid are in the Aleutian Islands, ~1600 km south of the Chukchi Sea, and its winter range is largely unknown (Gaston and Shoji, 2010). There are no records of Ancient Murrelets in the northern Chukchi Sea in the North Pacific Pelagic Seabird Database (USGS, 2010) in the ~35 years of data prior to 2007, and there are few records of these birds north of Bering Strait in the fall (Kessel, 1989). Surveys conducted by the USFWS, however, recorded 68 Ancient Murrelets in the Chukchi Sea in Sep/Oct 2007 (Kuletz et al., 2008),

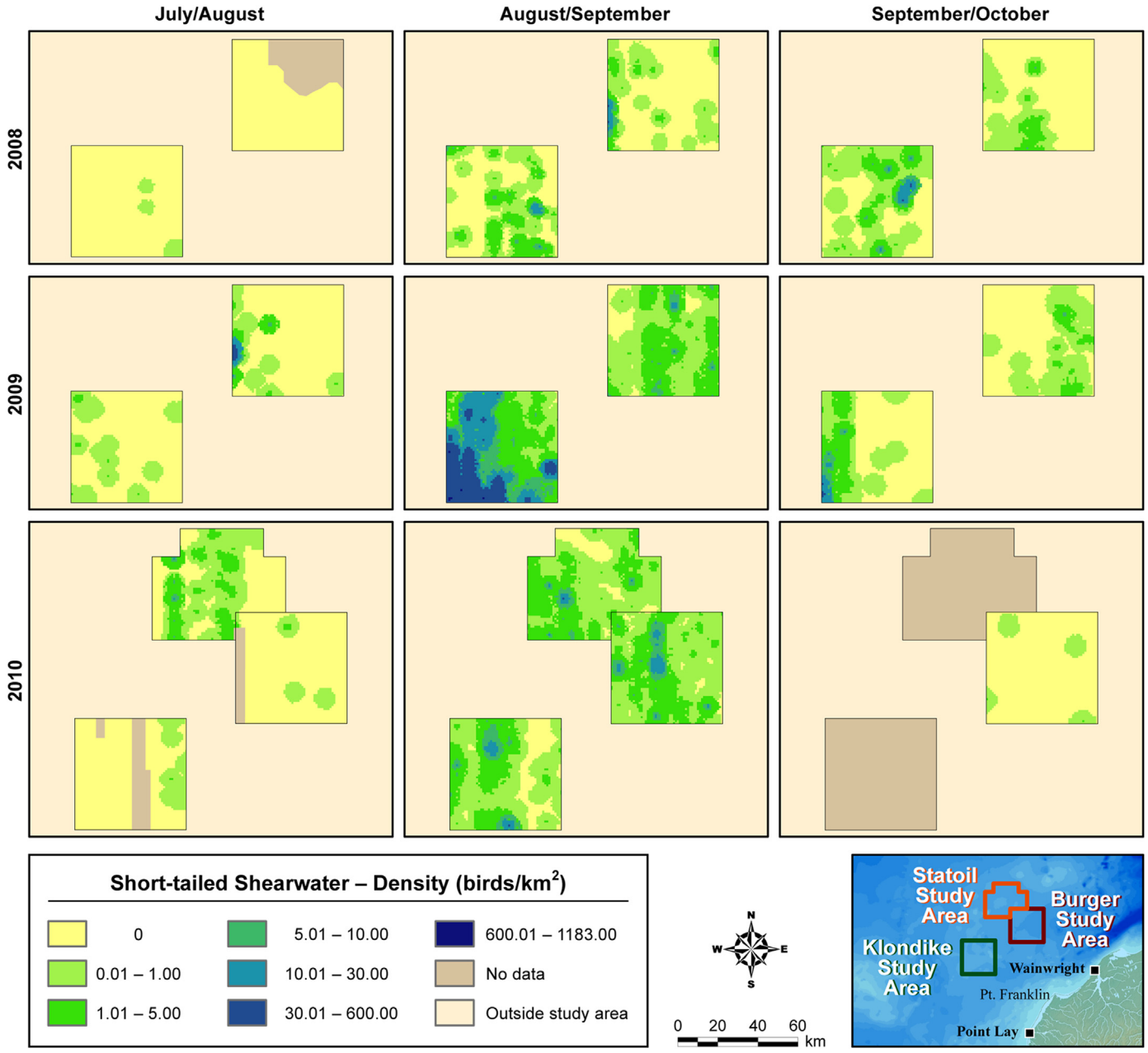

Fig. 15. Distribution of estimated densities (birds km^{-2}) of short-tailed shearwaters recorded on transect in the Klondike, Burger, and Statoil study areas of the northeastern Chukchi Sea in 2008–2010, by season and year.

suggesting that this species is an occasional visitor to the region and is common in years when it is present.

5.3. Conclusions

The 3 study areas in the northeastern Chukchi Sea collectively have a diverse marine-bird community of more than 30 species and, at times, maximal densities of >60 birds km^{-2} within a study area. There is extensive seasonal and interannual variation in the abundance of the seabirds in this area that is attributable primarily to planktivorous species. The greatest number of birds generally occurs in Aug/Sep (approximately 20 August to approximately 20 September), presumably reflecting a variety of factors that may include the timing of melt of sea ice, seasonal changes in the oceanography of the area, bird migration, nesting phenology and breeding success of birds in the Arctic. Despite this general seasonal trend, there is interannual variation in the timing of species-specific maximal abundance and this variation appears related to the strength and timing of inflow of Bering Sea Water from south of Bering Strait.

The scientific community is moving beyond describing this system to quantifying the spatial and temporal scales of processes in this region. We demonstrated that differences in the seabird community reflect oceanographic differences between Klondike and Burger, with Statoil representing elements of the other 2 study areas (Day et al., 2013). We propose that the Klondike study area is more of a pelagic-dominated ecosystem and the Burger study area is more of a benthic-dominated ecosystem, with Statoil tending to be more pelagic in its western half (the part nearest to the Central Channel; similar to Klondike) and more benthic in its eastern half (similar to Burger). Several other components of this multidisciplinary study also suggest a similar structuring of the ecosystem (Blanchard et al., 2013a, 2013b; Questel et al., 2013).

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at http://dx.doi.org/10.1016/j.csr.2012.11.004.

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